THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SECOND SERIES.]

No. 117. SEPTEMBER 1857.

XV.—*Researches on the mode in which Gum-Tragacanth is formed.* By Hugo von Mohl*.

The examination of Tragacanth gum possesses some theoretical interest, for it is connected with many difficult and as yet obscure points in the anatomy and physiology of plants.

Tournefort† was the first of those to whom we are indebted for exact observations on the secretion of gum-tragacanth from one of the plants furnishing this substance. His observations were made on *Astragalus creticus*, Lam., on Ida in Crete‡. According to the figure which he gives, the stem of the said tragacanth-plant attains a thickness of about 1 inch. The exudation of the tragacanth, in the form of coiled threads, takes place at the end of June and in the succeeding months.

Tournefort regarded tragacanth as the sap inspissated by the heat, which burst the vessels and poured itself out in the middle (*le cœur*) of the stem and branches, as well as in the medullary rays (dans l'interstices des fibres, lesquelles sont disposées en

* Botanische Zeitung, Jan. 16, 1857. Translated by Arthur Henfrey, F.R.S. &c.

† Relation d'un Voyage au Levant, i. 22. Amsterd. 1718.

‡ Sieber (Reise nach Kreta, ii. 68) has endeavoured to prove that Tournefort's statement is altogether incredible, for, according to his investigations in Crete, no tragacanth at all is secreted from the plant above named; but since not only Tournefort's statements regarding the parts of the stems in which the tragacanth is formed agree perfectly with my investigations, but his indication of the season at which the tragacanth exudes, as well as of the furtherance of the exudation resulting by making incisions in the stems, are confirmed by the observations made a century later by Olivier in Persia,—no one will be led to doubt, on such authority, Tournefort's statement that the said plant secretes tragacanth in Crete. When Sieber refers to the testimony of Belon, he makes a mistake, for Belon (Observat. p. 23) only says that no gum is collected on Mount Ida.

rayon), and as it was gradually driven out on the surface of the stem by fresh sap taken up by the roots, hardened in the air in the shape of worms. He adds further, the conjecture that contraction of the fibres of the stem assists in pressing out the gum, since the fibres, broken down into stringy masses, where exposed to be trampled on by sheep and horses, were contracted by heat, which would favour the emission of the sap.

These statements agree in many points with those of Olivier*, who observed the secretion of tragacanth from *Astragalus verus* in Persia.

In this species, also, the stem attained a thickness of an inch or more, and the gum exuded at the time of the greatest heat of summer, partly where the bark was split by the pressure of the sap, partly where the stem was injured by the tread of animals.

Further confirmation as to the season at which the tragacanth exudes from the stem is furnished by the statements of Labillardière and Landerer, the former of whom saw the gum excreted from *Astragalus gummifer*, Labill., in August, on Mount Lebanon; the latter, from *Astragalus aristatus*, in Greece, in August and September. In like manner, the statement that wounding the plants favours excretion of tragacanth, derives confirmation from the circumstance that in the district of Bitlis it is customary to make incisions in the plants for this purpose†.

Labillardière‡ mentions as an additional external circumstance favouring the exudation of tragacanth, moisture of the atmosphere, stating that, in Lebanon, cloudy nights and abundant dew are necessary for the excretion of the gum, and that this only exudes in quantity during the night, and for a short time after sunrise,—whence it happens that the shrubs growing on the lower part of Lebanon, which are exposed to very great heat by day, but receive little moisture at night, yield only a small quantity of tragacanth.

These statements of Labillardière are confirmed by the observations of Fraas§ in Greece, who states that no gum exudes (from *Astragalus aristatus* and *creticus*) on the higher mountains of the Peloponnesus, on Parnassus, or on dry mountains in general, while the gum is collected in Achaia. He regards the excretion of the gum as dependent on atmospheric influences, and ascribes it to the abundant cold rain with alternations of great heat, in the mountains of Calaryta, &c.

Labillardière drew, from the facts he observed, the conclu-

* Voyage dans l'Empire Othoman, 1807.
† Ritter, Erdkunde, x. 689.
‡ Rozier, Observations sur la Physique, &c., 1790, xxxvi. p. 48.
§ Synops. Plant. Floræ Classicæ, p. 39.

sion, that the tragacanth-shrubs, exposed to the glowing heat of the sun by day, rapidly absorbed the moisture of the clouds and fogs, and that the tragacanth, greatly swollen by the moisture of the fogs and dew, broke out through the pores of the bark, and exuded in the form of curled worms.

Labillardière's observation furnished DeCandolle* with an opportunity of explaining in a somewhat different manner the way in which tragacanth is squeezed out. He compared this exudation of tragacanth with that of *Nemaspora crocea* (which he at that time regarded as a gum, and not as a fungus) from the bark of the beech-tree, when kept in a damp place. He retained this view in his 'Physiologie' (i. p. 175), after he had recognized that *Nemaspora* was an independent plant, having convinced himself that the eruption of *Nemaspora* on dead trees was connected with the moisture of the atmosphere, and concluding from this that the action of moisture caused the wood to expand more than the bark; the wood being thus as it were compressed in a sheath, squeezed out upon the surface any slimy substance lying in the inner part of the bark. This explanation did not meet with any favour from Treviranus†, who assumed that the exudation of the gum depended upon increased secretion.

The botanists above mentioned, as also the most recent pharmacologists (for instance, Pereira) had not the slightest doubt that tragacanth was a mucilaginous juice secreted by the plant. Kützing‡, from the microscopic examination of exuded gum, set up the view that it was an independent organism, a fungus, composed of starch-bearing cells, among which lay the fibres of the parent-plant. The walls of these cells were described as consisting of many thick layers, composed of bassorin, and lined by a delicate membrane composed of cellulose. We look in vain for any proof that these cells are of Fungal nature; although such would be anything but superfluous, for Fungi with cellulose membranes and starch-granules would be not a little remarkable.

Unger§ ascribes a totally different origin to gum-tragacanth, stating that it is formed of the secondary layers of the medullary rays in several species of *Astragalus*.

I know of no other microscopic investigations of tragacanth which teach anything; those of Guibourt‖ are devoid of interest.

Seeking for an explanation of the nature of gum-tragacanth, I regarded it as of primary necessity to examine, not the gum occurring in commerce, but the stems of a large number of species of *Astragalus* of the section *Tragacanthæ*. Unfortunately

* Astragalogia, 1802, p. 12. † Physiologie, ii. p. 21.
‡ Philos. Botanik, i. 203. § Anat. u. Physiol. d. Pflanzen, 119.
‖ Hist. naturelle des Drogues simples, 4 edit. iii. p. 420.

my materials were so far imperfect that I possessed no thick stems, only such as were at most as thick as a little-finger, such as are found in herbarium specimens, on the bark of which no exudation of tragacanth was visible. The sequel will show, however, that this material was sufficient for the investigation of the mode in which the gum is formed.

The examination of excreted tragacanth is most instructively made in thin flat pieces. A transverse section of such a plate, swollen in water, exhibits abundance of thick-walled cells lying in an amorphous slimy mass. The walls of these cells are colourless, gelatinous, and formed of thick layers in part clearly separated from each other, so that in this respect they exhibit much resemblance to the laminated substance of a starch-grain. In the cavity of the cells lies a more or less considerable quantity of small starch-granules. Application of iodine is necessary for the exact investigation of these cells. It acts upon them very slowly, the iodized chloride of zinc solution producing no other alteration for several hours beyond colouring the starch-grains blue, and producing a slight yellow colour in the cell-walls. Distinct coloration of the cell-walls only commences after the solution has been in operation twenty-four hours or more. The thin innermost layer of the cell-walls is then found coloured bright violet, and isolated thin layers, of a more or less bright violet colour, are observed in the thick swollen cell-membrane, their thin, coloured laminæ being separated from each other by thick, colourless, gelatinous layers. The outermost of these coloured laminæ are frequently torn, in which case the colourless gelatinous substance has partly exuded through the rents, and become blended with the slimy substance in which the cells lie imbedded. From this partial solution of the outer layers, the magnitude of the cells, which are about ·07 millimetre in diameter, cannot be determined accurately, and many detached fragments of the blue iodine-coloured laminæ occur, scattered irregularly in the amorphous mucilaginous mass.

In tragacanth of the form of vermicular filaments, the cells were less perfectly preserved, and the amorphous mucilage in which the lighter and darker violet membranes and starch-granules were diffused, formed a relatively large portion of the entire mass.

In still smaller quantity did well-preserved remains of cells occur in Syrian tragacanth, having the form of nodular, yellowish fragments, in which, moreover, the quantity of starch-grains was far greater and their size more considerable, the granules being also frequently conglomerated in compound granules.

From the investigation of tragacanth gum I proceeded to the examination of the stems, which extended to all the following

species of the section *Tragacanthæ*: *Astragalus angustifolius*, Lam.; *aristatus*, L'Herit.; *Anacantha*, M. B.; *aureus*, Willd.; *Barba Jovis*, D.C.; *breviflorus*, D.C.; *bunophilus*, Boiss.; *campylanthus*, Boiss.; *caucasicus*, M. B.; *cephalanthus*, D.C.; *chromolepis*, Boiss.; *compactus*, W.; *creticus*, Lam.; *cyllenius*, Boiss. et Heldr.; *denudatus*, Stev.; *echinoides*, L'Herit.; *Echinus*, D.C.; *erianthus*, W.; *gossypinus*, Fisch.; *lagopodioides*, Vahl; *leiocladus*, Boiss.; *massiliensis*, L.; *microphysa*, Boiss.; *murinus*, Boiss.; *persicus*, Fisch. et Mey.; *plumosus*, W.; *Pseudo-tragacantha*, M. B.; *ptychophyllus*, Boiss.; *pychocephalus*, Fisch.; *pycnophyllus*, Stev.; *sciureus*, Boiss.; *siculus*, Biv.; *susianus*, Boiss.; *tumidus*, W. Among these occurred only four species in which no tragacanth-formation could be found in the stems, namely *A. aristatus*, L'Herit. (from the Pyrenees), *massiliensis*, L., *angustifolius*, Lam., and *echinoides*, L'Herit. In all the rest, tragacanth had made its appearance in more or less abundance*.

The structure of the stem in general is as follows. The wood is composed of thin annual layers, extremely tough, tearing easily in a longitudinal direction into slender fibres, enclosing a small pith, and traversed by pretty numerous medullary rays, exhibiting nothing unusual, as is the case with the bark also, which contains a well-developed liber and is clothed by a dense, tough periderm. The pith, on the other hand, and a large portion of the medullary rays, have a most striking characteristic, for, instead of presenting a thin-walled parenchymatous tissue, they appear to the naked eye in the form of a hard, transparent, gummy mass, and swell up into a jelly in water. On cut surfaces of the stem we frequently find a projecting mass of dry gum, which has exuded from the pith-cavity.

When we have recourse to the microscope, we perceive immediately that the gum-like mass which fills up the pith-cavity and the medullary rays, or has exuded from cut surfaces, does not consist of dried mucilage, but of the cells of the pith and medullary rays themselves, which have undergone a more or less complete transformation into gum-tragacanth.

Ordinarily this transformation has not affected all the cells of the pith and the medullary rays, but the outermost layers of the medullary rays, next to the wood-cells, regularly, and not unfrequently, in like manner, the outer part of the pith, lying against the woody bundles, are composed of ordinary thin-

* How far the subsequently described conversion of the cells into gum-tragacanth occurs in the species of *Astragalus* belonging to the other sections of the genus, I have not specially investigated; I may remark, however, that I observed the same transformation also in a couple of species of the section *Incani* which I took out at random, viz. *A. brachycarpus*, M.B., and *A. angulosus*, D.C.

walled parenchyma-cells, the membrane of which is coloured bright violet by the iodized chloride of zinc solution. These unaltered cells form, however, usually only a very thin stratum, composed of but a few cells, while all the rest of the cells constituting the central mass of the pith and of the medullary rays are metamorphosed.

That the peculiar character of these cells is a result of the transformation of ordinary parenchymatous cells, and not an original peculiarity of the cells of these parts, is shown by the fact, that the pith and medullary rays of the extremities of the shoots exhibit no unusual appearance.

The metamorphosed cells are distinguished from ordinary cellular tissue, in respect to their physical character, in that in a dry condition they form a very hard, transparent, gum-like mass, and in a wet condition a swollen slimy substance. Under the microscope these cells display, when their transformation has not advanced far, the angular forms and the close cohesion of parenchymatous cells, but their walls are very thick, and distinctly composed of many very thin laminæ; their primary membrane may be readily distinguished from the secondary layers of thickening, and is not thickened, as is seen in particular in cross-sections of the 'pits,' in which the primary membrane lies free. The whole form of these cells, the distinct lamination of their membrane, and the gelatinous softness of the latter in a wet condition, impart to them a great resemblance to the well-known cells of the cotyledons of *Schotia*.

In this stage of transformation into gum-tragacanth were, according to circumstances, either only those cells next in contact with the unaltered layers, or those also which formed the centre of the pith and the medullary rays; as I saw in young stems of *A. cyllenius*, Boiss., which, according to Orphanides, is one of those from which tragacanth is collected in Greece.

If the metamorphosis has advanced a step further, the individual cells swell up in a conical form in water, and become more or less completely isolated, retaining however their full integrity, no slime exuding from them into the water being rendered visible by the application of iodine.

In the last respect, however, I found a striking exception in some species (*A. aureus*, W.; *Pseudo-tragacantha*, M.B.; *compactus*, W.; *pycnocephalus*, Fisch.), for the cells were surrounded by an exuded slimy substance, apparently perfectly soluble in water, which immediately assumed a beautiful indigo-blue colour on the application of the iodized chloride of zinc. The same colour was produced in the amorphous contents of the cells, as also in the contents of the unchanged cells of the medullary rays, and of a part of the cortical cells. But this coloration was

transitory, for in the course of a few hours the blue colour had entirely vanished, and a yellowish tint remained. This phænomenon again reminds us of the cotyledons of *Schotia*, from which in like manner exudes a slimy substance coloured bright blue by iodine and coagulable by alcohol. In other cases, in particular in *A. cyllenius*, the metamorphosed cells discharged into the water a slimy substance coloured yellow by iodine; both this, however, and the slime coloured blue by iodine, are exceptional.

When the transformation of the cells into gum-tragacanth has advanced farther, the membrane which swells up strongly in water is no longer distinctly seen to be composed of numerous thin laminæ. This conversion into a mass, of homogeneous aspect, advances from without inwards in the cell-membrane; for I saw (in *Astragalus murinus*) cells in which this affection had attacked the outer half of the cell-wall, while the inner half, separated from the outer homogeneous mass by a sharp line, still displayed the fine lamination.

The final conversion into perfect tragacanth results when the cells lose their external solid boundaries, and their outer laminæ coalesce into a more or less uniform slimy mass; in which, as is frequent in exuded gum, the inner laminæ may still exist in perfect integrity.

The cells metamorphosed in the above-described manner exhibit, at least when wetted, a considerably greater diameter than the thin-walled cells from which they originate: thus, one of the large unaltered cells of the medullary rays of *Astragalus denudatus* is ·0064 of a millimetre in diameter, while a metamorphosed but still distinctly defined cell from the interior of the same medullary ray measures ·035 millim., that is, about five times the size; in *A. Echinus* the size of the metamorphosed cells of the pith amounted to ·06 of a millimetre, and had thus reached about the magnitude of the cells contained in tragacanth which had exuded from the stem.

The behaviour of the cells with iodine alters in proportion to the degree of metamorphosis they have undergone. The unchanged cells of the pith and medullary rays assume a deep violet colour with the iodized chloride of zinc solution in the space of twenty-four hours. The cells which have been only slightly altered, and have still the form of angular but thick-walled prosenchymatous cells, are likewise coloured deep violet. But this colour is not uniform throughout the whole thickness of the cell-wall, the innermost and outermost laminæ being especially brightly coloured, while solitary thin lamellæ among the secondary layers exhibit a violet tint. I could not determine whether the uncoloured laminæ between these coloured layers were

perfectly colourless or tinged with a very light violet colour. A similar condition is well known to occur frequently in other thick-walled parenchyma-cells which become softened and greatly swollen when placed in water; for instance, in those of *Schotia*.

The further the dissolution of the cells and their conversion into gum-tragacanth proceeds, the lighter is the violet colour assumed by the entire mass of them, since the uncoloured or slightly tinted laminæ more and more exceed in proportionate dimensions; and even the coloured laminæ, especially the outer, perhaps simply as a result of greater mechanical expansion, exhibit a lighter colouring.

The described observations will leave no doubt of the fact that gum-tragacanth is neither a secreted sap dried by exposure to the atmosphere, nor an independent Cryptogamic organism, but that its formation depends upon a more or less perfect transformation of the cells of the pith and medullary rays into a gelatinous mass, which swells up to many hundred times the original size of the cells when placed in water.

Whether the production and expulsion of the gum occur but once in one and the same part of the stem, or are repeated during many years, can of course be determined only in the native country of the tragacanth-plants; perhaps, however, the conjecture that it is a process persisting through an extended period is not too bold. The transformation of the pith can of course only occur once in any given part of the stem, and this source will be extinguished with the earlier or later expulsion of the gum formed. But the case may be otherwise with the medullary rays, since all the medullary rays of any particular part of the stem do not undergo their metamorphosis at the same time. In the younger of the stems examined by me, at least only a portion of the medullary rays had undergone this change, while the rest still displayed the usual constitution of thin-walled cells. It may be indeed assumed, from the great firmness of the periderm clothing the stem, that the breaking-out of the gum through the bark takes place annually from only a small portion of the medullary rays, and thus perhaps goes on for many years, until all the medullary rays of a length of the stem have been emptied.

Surveying the vegetable kingdom, with a view to ascertain whether analogous conversions of cells into mucilage occur elsewhere, we find similar processes to be anything but rare. Attention has been especially directed by Alex. Braun* to the fact of an exactly corresponding softening of the cell-membranes,

* Verjungung, p. 203. Ray Society's Memoirs, 1853, p. 189.

a swelling-up in a gelatinous form, terminating in their dissolution, being a very ordinary phænomenon in the families of Palmellaceæ, Chroococcaceæ, and Nostochineæ; that analogous changes of the cell-coats occur in *Hydrodictyon* and *Botrydium*; and that the gelatinous softening of the membrane of the parent-cells of pollen-grains also stands in connexion with their subsequent solution. In like manner I have satisfied myself that the abundant 'intercellular substance' in the albumen of many Leguminosæ, such as *Gleditschia* and *Sophora*, depends on an exactly analogous process, on a conversion of the outer laminæ of the cell-walls into a homogeneous jelly, in which latter an indication of the primary membrane may often be detected for a long time, till at length it vanishes, and leaves no trace. I have also no doubt that the formation of the 'intercellular substance' of the Fucoids, of *Chondrus crispus*, &c., depends upon exactly analogous processes. We have therefore to regard the formation of gum-tragacanth as a special example of a widely diffused disorganization-process of cell-membrane, which proceeds from without inwards, sometimes affecting the whole cell-wall, sometimes only the outer laminæ, and terminates in the conversion of the membrane into a more or less soluble jelly. On the other hand, it appears to me less proper to draw a parallel, with Unger, between the formation of gum-tragacanth and the formation of the secondary and tertiary gelatinous cell-membranes, such as occur in the seed-coats of *Cydonia*, *Linum*, *Collomia*, *Ruellia*, &c.; at all events, it is not known to me that these exist in the condition of cellulose-membrane previously to the period in which they are found with the character of gelatinous pellicles.

Tubingen, Dec. 1856.

[*Note of Translator.*—With regard to the remarks in the last paragraph, we find the 'swelling-up' coats of the hairs of *Collomia*, *Ruellia*, &c., to be the metamorphosed *outer* membranes, which take a violet colour with sulphuric acid and iodine when dissolved into a mere jelly, while the spiral fibres or rings (secondary deposits) are coloured yellow. Hence we regard these structures as parallels of the cell-membrane of tragacanth. The author's view of the structure of the horny thallus of *Chondrus* is entirely confirmed by our own examinations of the tissue in various stages of development.—A. H.]